

BREEDING RESPONSES OF RAPTORS TO JACKRABBIT DENSITY IN THE EASTERN GREAT BASIN DESERT OF UTAH

by

Dwight G. Smith

Department of Biology

Southern Connecticut State College

New Haven, Connecticut 06515

and

Joseph R. Murphy

Department of Zoology

Brigham Young University

Provo, Utah 84602

Abstract

The relationships between a collective breeding raptor population of the Golden Eagle (*Aquila chrysaetos*), the Great Horned Owl (*Bubo virginianus*), the Ferruginous Hawk (*Buteo regalis*), and the Red-tailed Hawk (*Buteo jamaicensis*) and its main prey base, the black-tailed jackrabbit, is examined. By biomass, the jackrabbit is the single most important food item in the diet of each of the raptor species. Populations of each raptor species varied synchronously with jackrabbit abundance. Excepting Red-tailed Hawks, reproduction and operative breeding season mortalities were influenced by jackrabbit abundance. The role of the central Utah environment in dictating patterns of raptor response to its staple prey base is considered.

Introduction

Solomon (1949) proposed that predators respond to prey fluctuations in two distinctive ways, functionally and numerically. The functional response involves a change in food consumed by the individual predator. The numerical response involves an increase in predator density as prey increases, usually through recruitment by immigration and increased predator reproduction.

In this paper we examine the relationships between the breeding population dynamics of a collective raptor population consisting of the Golden Eagle (*Aquila chrysaetos*), the Great Horned Owl (*Bubo virginianus*), the Ferruginous Hawk (*Buteo regalis*), and the Red-tailed Hawk (*Buteo jamaicensis*) and abundance of their main prey base, the black-tailed jackrabbit (*Lepus californicus*).

The study was conducted from November 1966 through August 1970. Some additional observations were also made during the late spring and summer months of 1971 and 1972. Data similar to that which we give here are presented by Woffinden and Murphy (1977) for 1973 and 1974 for the same study area.

The exact nature of the response to changing prey densities remains unclear for many raptor species. Nicholson (1930) and Pitelka et al. (1955 a, b) have shown that tundra-inhabiting raptors exhibit strong numerical and functional responses to a cyclic and limited prey base. Responses of temperate raptor populations may be less dra-

matic. In Alberta, McInville and Keith (1974) reported that Great Horned Owls, but not Red-tailed Hawks, showed changes in breeding season density and food habits occurring synchronously with snowshoe hare (*Lepus americanus*) populations. Although Craighead and Craighead (1956) concluded that raptor population densities in Michigan tended to remain relatively stationary, the situation elsewhere is largely unknown.

Study Area

We began long term raptor studies on a 7,700 km² portion of the eastern Great Basin Desert in winter 1966. Initial studies in 1966–1968 focused primarily on Golden Eagles, Great Horned Owls, and Ferruginous Hawks (Murphy et al. 1969). Additional information on these and the Red-tailed Hawk was presented in a four-year collective raptor study on a smaller, 207 km² intensive study area (Smith and Murphy 1973). Herein we analyze raptor-jackrabbit relationships on a 1,170 km² portion of the original study area.

Topographically, the area is characterized by broad, flat alkaline valleys separated by high, north-south running ridges and hills. Valley elevations range from 1,460 to 1,620 m, and maximum elevations of the ridges and hills range from 1,830 m to upwards of 2,440 m.

Climatically the area is characterized as a northern cold desert (Shelford 1963). Annual precipitation averages 38 cm, and mean monthly temperatures range from -5°C in January to 24°C in July with wide daily and seasonal variations.

Two distinctive vegetation associations occur, the mountain desert shrub community and the dwarf conifer community. The desert shrub community is present over the lower elevations and on the valley floors. It consists of mixtures of shrubs, herbs, and grasses, several of which may, under certain edaphic soil conditions, form large communities. Two predominant shrub communities thus formed include big sagebrush (*Artemisia tridentata*) on the better drained soils, and greasewood (*Sarcobatus vermiculatus*) on the poorly drained valley floors. The well-drained slopes and hills support a dwarf conifer community of Utah juniper (*Juniperus osteosperma*) and pinyon pine (*Pinus monophylla*) which occur in stands of widely varying density.

This part of the Great Basin has a history of chronic livestock over-grazing which dates from the late 1800s. This circumstance coupled with extensive state and federal predator-control programs, has produced conditions which allowed jackrabbit populations to drastically increase periodically to the point at which they are considered a major range pest species (Stoddard et al. 1975).

Methods

Jackrabbit Populations. We determined jackrabbit abundance by (1) transect counts, (2) road kill counts, and (3) queries of local ranchers and stockmen.

Permanent linear transects, each 805 m in length, were marked off through six large desert scrub communities selected at random in the study area. Vegetation of the transects included typical predominant vegetation of the study area. At biweekly intervals from mid-December through March all transects were walked by two observers spaced 20 m apart. Counts derived from transects are indications of relative abundance rather than absolute population counts and reflect the basic weakness of the transect method (Southwood 1966). They do, however, provide adequate indices of population change (Gross et al. 1974) and were the only practicable means of esti-

mating jackrabbit population abundance over our large study area.

Each year we recorded winter monthly tallies of the number of local kills observed on nearby highways. Such a tally is a rough but useful index, especially when used in conjunction with other methods.

Each year we asked resident ranchers and stockmen and itinerant hunters to estimate and compare jackrabbit abundance with previous years. This questioning provided subjective information which may at the very least indicate high and low years of jackrabbit abundance.

Raptor Populations. From November 1966 through August 1970 we visited the study area at least once and usually two or more times per week to obtain information on raptor population dynamics. The 207 km² intensive study area was divided into subsections, each approximately 1.6 km², to facilitate survey. These were systematically searched in a rotating sequence for raptor nesting pairs, nonnesting pairs, and individuals at biweekly intervals beginning in mid-December and lasting through mid-May of each year.

Foot searches were supplemented by aerial surveys, but the latter were of limited usefulness because of minimum speed and altitude requirements.

Status of nesting pairs, nonnesting pairs, and single birds on the intensive study area was checked at least twice weekly during the nesting season and once weekly on the 1,170 km² study area. Throughout the four breeding seasons the single exceptional time interval between successive study area visits was 13 days in April 1970.

Raptor Food Habits. Food habits of each raptor species were determined by weekly tabulations of prey items and analysis of pellets gathered from the nest site. Prey remains were usually left on the nest, after being marked by toe clipping to avoid duplication in tabulation.

Results

Jackrabbit Populations. Jackrabbit numbers were low in 1967 and 1970, intermediate in 1968, and high in 1969 (fig. 1). The average number of individuals per transect count each year were: 1967, 3.3 ± 0.7 (range 0–7 individuals); 1968, 9.03 ± 1.2 (ranges 3–17); 1969, 13.8 ± 1.5 (ranges 6–31); and 1970, 3.6 ± 1.0 (ranges 0–9). Winter road kill counts in terms of individuals per mile of road travelled for each of the study years are: 0.8 in 1967; 1.4 in 1968; 1.9 in 1969; and 1.1 in 1970.

Subjective observations by local stockmen, ranchers, and sportsmen familiar with the study area also suggest that jackrabbit populations peaked in 1969 and declined in 1970. Our own data plus casual observations indicate that jackrabbit abundance peaked in 1969 and declined in 1970. In 1969, for example, we commonly were able to observe concentrations of 50–75 individuals feeding in small open fields of 3–5 acres during the late evening hours after sunset.

While none of these results provide conclusive evidence of jackrabbit population fluctuations, they do, considered together, strongly suggest that populations of 1968 and 1969 were considerably larger than populations of 1967 and 1970. Gross et al. (1974) conducted a separate study of jackrabbit populations approximately 200 km north of our study area. Their estimates of jackrabbit densities as determined by transects and drive counts, show a similar population low in 1967 followed by increasing population densities in 1968 and 1969. They did not find a corresponding decline in 1970 but did observe that synchrony of intermountain valley populations were in some instances 1–2 years out of phase with one another.

Avian Predator Food Habits. We have previously described the food habits of each of the avian predators (Murphy et al. 1969, Smith and Murphy 1973, and in press) and herein present only brief summaries (table 1). On a weight basis the black-tailed jackrabbit was the single most important prey item of each raptor species, contributing from a minimum of 81.6% to a maximum of 94.1% of the prey biomass con-

Table 1. Abridged food habits summaries of breeding raptors, 1967-1970.

	1967			1968			1969			1970		
	% No.	% Biomass ¹	% No.	% Biomass	% No.	% Biomass	% No.	% Biomass	% No.	% Biomass	% No.	% Biomass
Golden Eagle												
<i>Lepus californicus</i>	64.0	88.8	82.0	94.1	76.8	90.7	52.5	81.1				
<i>Sylvilagus</i> sp.	17.3	10.5	11.3	5.6	17.8	9.2	25.9	17.4				
Other Mammals	14.7	0.5	5.3	0.2	4.6	0.1	19.4	0.8				
Birds	4.0	0.2	1.5	tr ³	0.8	tr	2.1	0.7				
Totals ²	75	124360	87	266320	241	469375	139	206945				
Great Horned Owl												
<i>Lepus californicus</i>	23.3	81.6	42.4	89.4	66.1	90.2	47.5	87.0				
<i>Sylvilagus</i> sp.	9.3	12.3	8.2	7.6	14.6	8.7	13.7	10.9				
<i>Dipodomys</i> sp.	43.0	3.8	35.3	2.2	7.3	0.3	18.6	1.0				
Other Mammals	18.6	1.5	12.9	0.7	7.3	0.3	15.3	0.7				
Birds	5.8	0.7	1.2	0.2	4.7	0.2	4.9	0.4				
Totals	86	64789	85	92605	316	530711	183	229913				
Ferruginous Hawk												
<i>Lepus californicus</i>	42.0	93.7	38.6	92.3	52.4	94.0	50.0	92.2				
<i>Sylvilagus</i> sp.	2.7	2.6	2.8	2.9	4.1	3.3	6.7	5.4				
<i>Dipodomys</i> sp.	32.1	2.2	35.8	2.5	18.2	0.9	20.1	1.1				
Other Mammals	11.5	1.3	15.3	1.7	14.3	1.3	12.0	0.7				
Birds	5.4	0.1	6.4	0.3	9.1	0.2	9.2	0.2				
Reptiles	6.3	0.1	1.1	0.3	1.9	0.3	2.0	0.4				
Totals	112	115366	285	273971	307	393757	194	242080				
Red-tailed Hawk												
<i>Lepus californicus</i>	39.7	87.9	43.4	88.6	56.1	92.3	41.3	89.2				
<i>Sylvilagus</i> sp.	9.0	8.6	10.1	8.9	8.5	6.1	8.4	7.9				
Other Mammals	42.3	2.5	30.2	1.6	25.9	1.1	39.7	2.2				
Birds	6.4	0.7	14.7	0.8	6.6	0.2	8.9	0.4				
Reptiles	2.6	0.3	1.6	0.2	2.8	0.3	1.7	0.3				
Totals	75	81090	129	145410	212	296660	179	190740				

¹Weight in grams from Smith and Murphy (1973).
²Percent of total weight of prey.
³tr = trace, less than 0.1 percent.

sumed. This finding supports the contention of Clark (1972) that jackrabbits form a major part of the food base of the northern cold desert ecosystem.

On a percent frequency basis, however, some differences in prey species occurrence are evident between high prey years (1968 and 1969) and low years (1967 and 1970). Chi-square tests of the frequency of occurrence of each of the prey categories reveal significant statistical differences between years ($P < 0.01$) in Ferruginous Hawk and Red-tailed Hawk food but not for that of Great Horned Owls or Golden Eagles, although the two latter raptor species exhibit some diet differences. These differences in food between high- and low-jackrabbit years suggest a shift to alternate or buffer prey species. The observed degree of shift to alternate species was, however, not commensurate with the decline in jackrabbit abundance, and this prey species still comprised 82% or more of the food biomass of each raptor species even in low-jackrabbit years.

We believe that the abundance of jackrabbits is thus an important limiting factor which largely determines annual changes in the size and reproductive performance of the collective raptor breeding population.

Avian Predator Populations. A summary of yearly raptor population trends is presented in table 2. The annual breeding-season populations of the four species were approximately, in order of most to least common: *Buteo regalis*, *Bubo virginianus*, *Aquila chrysaetos*, *Buteo jamaicensis*. Each year pairs of another large raptor, the Swainson's Hawk (*Buteo swainsoni*), were consistently present on the study area, but were too few in number to permit detailed analysis.

The correlation between the raptor population and jackrabbit abundance is readily evident and may be categorized as the first component of numerical response. Total numbers of raptors in low-jackrabbit years varied from 18–49% below populations of high-jackrabbit years. The magnitude of change is illustrated by 1967 (a low year) and 1969 (a peak year) populations, in which almost twice as many raptors were found on the study area.

Populations of Golden Eagles and Great Horned Owls, both permanent residents, showed comparatively less yearly variation than the migratory Ferruginous Hawk and Red-tailed Hawk populations. Thus, after an initial increase from 1967 to 1968, Golden Eagle numbers varied only by 3 and Great Horned Owl numbers by 4 during the three years, 1968–1970. In contrast Ferruginous Hawk numbers changed considerably over the four-year period, with the 1969 population about one-third larger than 1968 and about twice as large as 1967 and 1970 populations. The observed recruitment of Ferruginous Hawks is probably to some extent a function of its migratory status. Studies by Craighead (1959), Naumou (1948), Galushin (1974), and others have noted the ability of several nomadic avian predator species to concentrate rapidly in areas of prey abundance. Pitelka et al. (1955 a, b) reported large variations in the highly mobile raptor populations of the Arctic tundra, and Linkola and Myllymaki (1969) observed invasions of certain raptor species during high-rodent years in Finland. Comparatively, the strongly territorial and permanently resident Tawny Owl (*Strix aluco*) was noted by Southern (1970) to maintain relatively stable numbers from year to year on his Wytham Wood Study Area in England.

Breeding Fraction of the Avian Predator Population. The tendency of pairs to breed or refrain from breeding may be considered as a part of the second component of nu-

Table 2. Raptor population trends in central Utah, 1967-1970.

Raptor Species	1967	1968	1969	1970
Golden Eagle				
No. pairs	9	14	14	13
No. breeding pairs	7	13	13	11
No. single birds	1	1	1	0
Total no.	19	29	29	26
Great Horned Owl				
No. pairs	7	16	16	13
No. breeding pairs	6	14	16	10
No. single birds	2	1	1	3
Total no.	16	33	33	29
Ferruginous Hawk				
No. pairs	19	31	38	20
No. breeding pairs	15	28	34	13
No. single birds	5	1	2	4
Total no.	43	63	78	44
Red-tailed Hawk				
No. pairs	8	12	13	12
No. breeding pairs	5	10	12	11
No. single birds	1	0	1	0
Total no.	17	24	27	24
Totals (All Species)				
No. pairs	43	73	81	58
No. breeding pairs	33	65	76	45
No. single birds	9	4	5	7
Total no.	95	149	167	123

merical response, which includes all strategies directed towards increasing predator population growth. We classified a pair as breeding if a nest was constructed and attended. For the collective raptor population, the ratio of breeding pairs to total pairs varied synchronously with jackrabbit abundance. Percentage ratios (pairs breeding to total pairs present) were 76.7% and 77.6% for the low-jackrabbit years of 1967 and 1970 respectively, 89.0% for the intermediate year 1968, and 93.8% for the peak-jackrabbit year of 1969. Only one species did not follow this pattern: the number of Red-tailed Hawk breeding pairs in 1970 was one larger than in 1968, although lower than in 1969.

In studies elsewhere, Hamerstrom (1969), Pitelka et al. (1955 a, b), and Rusch et al.

(1972) all reported increased percentages of breeding pairs of raptors during high-prey years, which contrasted sharply with a low intensity of nesting efforts in low-prey years. Southern (1970) found that the percentage of Tawny Owl pairs which each year attempted to breed varied from zero in unfavorable years to 87% in high-rodent years. He further observed that the most common way in which Tawny Owl pairs reacted to low prey was by refraining altogether from breeding.

Pairs which have constructed and attended a nest may lay their eggs or, conversely, refrain from depositing eggs and subsequently desert the nest. We did find a slightly higher incidence of nest desertion in low prey years, but unfortunately the question of possible human interference, not uncommon in our study area, renders analysis of this relationship unclear. It is quite possible, however, that pairs attempting to breed in times of low prey are more intolerant of disturbance. In favorable years breeding pairs appeared to be far more tolerant of our activities in the vicinity of the nest site (cf. Woffinden 1975 for data on this aspect).

Clutch Size. Mean clutch size of Golden Eagles, Great Horned Owls, and Ferruginous Hawks, but not Red-tailed Hawks, varied in synchrony with rodent density (table 3). Clutches of Golden Eagles varied from 1.9 in low years to 2.2 in peak years. The 1968 and 1969 clutches of Great Horned Owls and Ferruginous Hawks tended to contain a minimum of one additional egg as compared to 1967 and 1970 clutches ($t=2.58$; 2.75 respectively, $P<0.05$ for both), but not significantly different from one another ($t=1.26$; $P>0.05$). In addition, mean clutch size of 1967 and 1970 did not differ significantly ($t=1.15$; $P>0.05$). Similarly Ferruginous Hawk clutches of 1968 and 1969 were significantly larger than 1967 and 1970 clutches ($t=2.56$; 2.92 respectively; $P<0.05$) but not different from one another ($t=0.11$; $P>0.05$). Again, clutches of 1967 and 1970 did not differ significantly ($t=0.11$; $P>0.05$).

McInville and Keith (1974) found a significant increase in Great Horned Owl clutch size during years of high snowshoe hare abundance, and Houston (1971) determined that the largest brood sizes of this nocturnal avian predator coincided with years in which its prey was most abundant.

Unlike the other raptor species, clutch size of Red-tailed Hawks consistently increased each year, from a low of 2.5 in 1967 to a high of 3.3 in 1970. In contrast, McInville and Keith (1974) found that peak clutch size of Red-tailed Hawks near Alberta did occur simultaneously with highest annual snowshoe hare abundance.

For three of the four species the combination of increased numbers of breeding pairs and large clutches resulted in a greater total productivity of eggs in years of jackrabbit abundance. Correlation tests reveal a significant relationship between prey abundance and total egg production of Great Horned Owls ($r=0.97$; $t=5.24$; $P<0.05$) and Ferruginous Hawks ($r=1.98$; $t=6.64$; $P<0.05$). Total egg production of Golden Eagles and Red-tailed Hawks was slightly greater in 1968 and 1969, but the relationships are not significant ($P>0.05$ for both species).

Fledged Brood Rates. Reproductive success as measured by fledged brood rates varied considerably among the raptor species. A clear correlation between total number of fledged young, nesting success (percentage of young fledged per eggs laid), and jackrabbit abundance can be observed only for Ferruginous Hawk populations. Great Horned Owl fledged brood rates were considerably higher in favorable years, but percentage breeding success was lower in those years. To complicate the problem, the fledged brood production of Red-tailed Hawks was generally higher in favorable years, despite the increased clutch size in 1970, which was offset by increased morta-

lity of young in the nest. A major factor contributing to greatly fluctuating mortality rates from hatching to fledging is the comparatively high level of human disturbance affecting many avian predator pairs on our study area. Golden Eagles, the largest and most conspicuous of the diurnal raptors, were frequently the object of such activities as egg collecting, photography of young, deliberate nest destruction, and attempts by hunters to kill the adults. These disturbances, of course, render any analysis of yearly breeding success unrealistic unless their effect on the behavior of the birds can be resolved.

Table 3. Reproduction of large raptors in central Utah, 1967-1970.

Raptor Species	1967	1968	1969	1970
Golden Eagle				
No. clutches produced	7	13	13	11
Av. clutch size	1.9	2.0	2.2	1.9
Total eggs produced	13	26	27	21
No. nests hatching young	5	12	10	10
No. young hatched/nest	1.2	1.2	1.2	1.8
Total young hatched ¹	6 (46.2)	15 (57.7)	11 (40.7)	18 (85.7)
No. nests fledging young	5	11	9	10
No. young fledged/nest	0.8	0.9	1.0	1.7
Total young fledged ²	4 (30.8)	10 (38.5)	9 (33.3)	17 (81.0)
Great Horned Owl				
No. clutches produced	6	13	15	10
Av. clutch size	2.0	2.9*	3.3**	2.4
Total eggs produced	12	38	50	23
No. nests hatching young	5	12	14	8
No. young hatched/nest	1.8	2.5	2.7	2.3
Total young hatched	9 (75.0)	30 (78.9)	38 (76.0)	19 (82.6)
No. nests fledging young	5	11	13	8
No. young fledged/nest	1.8	1.9	2.4	1.8
Total young fledged	9 (75.0)	21 (55.3)	31 (62.0)	15 (65.2)
Ferruginous Hawk				
No. clutches produced	14	28	34	12
Av. clutch size	2.5	3.7**	3.8**	2.9
Total eggs produced	36	104	129	35
No. nests hatching young	11	25	32	9
No. young hatched/nest	1.3	2.4	3.1	1.4
Total young hatched	15 (41.7)	60 (57.7)	99 (76.7)	17 (48.6)
No. nests fledging young	10	25	31	7
Total young fledged/nest	1.2	2.2	2.9	1.4
Total young fledged	12 (33.3)	55 (52.9)	90 (69.8)	10 (28.6)

Red-tailed Hawk

No. clutches produced	5	10	12	11
Av. clutch size	2.5	2.8	3.1	3.3
Total eggs produced	13	28	37	36
No. nests hatching young	5	9	11	11
No. young hatched/nest	1.8	2.3	2.5	2.3
Total young hatched	9 (69.2)	21 (75.0)	28 (80.0)	26 (72.2)
No. nests fledging young	5	9	10	9
No. young fledged/nest	1.5	1.6	2.2	1.5
Total young fledged	8 (61.9)	15 (53.6)	22 (59.5)	14 (38.9)

¹Figures in parentheses are percentages of total eggs hatched to total eggs laid.

²Figures in parentheses are percentages of total young fledged per total eggs laid.

*Significant at P<level.

**Significant at the P<0.01 level.

Discussion

Breeding Mortality and Regulation of Avian Predator Populations. If we arbitrarily allow that the maximum reproductive potential of the collective raptor population (excepting Red-tailed Hawks) was achieved during the peak prey year of 1969, then we may comparatively measure the limiting effects of declining prey populations on raptor reproduction. Several factors decreased breeding productivity during unfavorable years (or conversely, increased mortality). Among these were: (1) failure of pairs to nest, (2) failure of pairs to achieve maximum clutch size, and (3) failure to hatch brood, and fledge a maximum number of young. These mortality factors are related in sequential fashion. Thus, for a breeding avian predator population to have a productive year there must be a certain minimum prey density which provides the stimulus and physiological ability to breed. Further increases in prey density may be reflected in increased productivity, up to the point at which other resources may become limiting. Conversely, lower prey densities inhibit breeding and increase the probability of mortality at all breeding stages.

Southern (1970) has shown that the relationships between breeding mortalities and prey abundance may be examined by key factor analysis. This technique, developed by Varley and Gradwell (1960) and critically discussed by Ito (1972), permits inspection of the contribution of each mortality (k_i) to the total mortality (K) acting on the population.

We confined our key factor analysis to the sequence of mortality operating on the following phases of the breeding population:

- (1) k_1 = logarithm of maximum eggs producible by maximum-sized breeding population—logarithm of the number of eggs produced by the actual-sized breeding population.

The maximum breeding season population of each avian predator species was attained in 1969, and k_1 measures the mortality increase in other years when the respective species did not achieve the 1969 breeding population level. In effect, k_1 is a measure of the mortality produced by a pair's decision to breed or forgo breeding, which we believe, will be a function of available food resources.

- (2) k_2 = logarithm of eggs produced with all breeding pairs achieving maximum average clutch size—logarithm of actual number of eggs produced by breeding pairs.

The yearly average clutch size is measured against the maximum yearly average clutch size achieved. Three species attained a maximum in 1969: Golden Eagle, 2.2; Great Horned Owl, 3.3; Ferruginous Hawk, 3.8. Red-tailed Hawk maximum average clutchsize of 3.3 occurred in 1970; it was 3.1 in 1969.

(3) $k3$ = logarithm of eggs actually laid—logarithm of eggs which subsequently do hatch

This key factor measures the mortality caused by the proportion of eggs laid which do not hatch, regardless of specific cause.

(4) $k4$ = logarithm of the number of young which hatch—logarithm of the number of young which fledge.

This mortality factor measures the impact of loss of young which have actually hatched but for whatever reason do not fledge.

(5) $K = k1 + k2 + k3 + k4$

K will thus represent the absolute impact of the four stages of mortality which occur during the nesting sequence.

Results of key factor analysis for each raptor species are presented in figure 2. Although key factors are occasionally subjected to statistical treatment, Eberhardt (1970), Ito (1972), and Kuno (1973) have all suggested defects of regression analysis which may distort and invalidate results. We support their conclusions and restricted our analysis to graphical inspection, similar to that of Varley and Gradwell (1960).

Inspection suggests that the two most important mortality factors operative on Great Horned Owl populations are $k1$, the failure of a maximum number of pairs to nest, and $k2$, the failure of nesting pairs to achieve maximum clutch size. The graph of $k4$, the mortality of hatched young, diverges synchronously from K and suggests that $k1$ and $k2$ mortalities are at least partly compensated by increased survival of young in poor prey years.

Mortality factors $k1$ through $k3$ are equally additive in impact on Ferruginous Hawk reproduction. Factor $k4$ also follows K , albeit weakly. The close graphical correlation of $k1$ – $k4$ mortality factors with K suggests that Ferruginous Hawk reproduction is strongly influenced in a density-dependent manner by jackrabbit abundance.

Graphs of key factors operative on Golden Eagle populations are less readily interpreted. Although failure of maximum pairs to nest plus achieve maximum clutch size was contributory, $k3$, the failure of eggs to hatch, was the single most important mortality factor. Unfortunately, the previously discussed high level of human disturbance of Golden Eagle nests may have contributed to the importance of this mortality factor.

Graphs of Red-tailed Hawk $k1$, $k2$, and $k4$ factors partially paralleled K , suggesting that Red-tailed Hawks may have partially adjusted their reproduction to jackrabbit abundance in density-dependence fashion. The $k3$ mortality partially diverges in compensatory fashion. The overall relationships between Red-tailed Hawk reproduction and jackrabbit abundance, however, remain unclear. Red-tailed Hawk food habits during low prey years did show a higher utilization of alternate prey species as compared to the other large raptors (table 1), and it is possible that this usage of other prey was fully commensurate with jackrabbit decline.

Nature of the Predator-Prey Relationship. The nature of the relationship between the large avian predators and their stable prey base in central Utah warrants further consideration. Luttich et al. (1970) have suggested that regional raptor populations

may exhibit different adjustment patterns to a fluctuating prey base. They note that the staple prey base of the North is limited to just a few species of highly cyclic microtine rodents that Arctic raptors tend to concentrate upon and effectively exploit. They compare this response to temperate-zone raptors, which maintain notably stationary local populations, despite fluctuating prey abundance, and instead vary reproduction with prey abundance.

The large raptor populations of central Utah appear to combine elements of both response patterns. Thus, populations of each raptor species increased in high-jackrabbit years and decreased in low-jackrabbit years, suggesting that even the permanently resident populations of Golden Eagle and Great Horned Owls are in fact able to shift into an area of prey abundance. In central Utah, this ability to concentrate upon and exploit local prey abundance is most dramatically illustrated by the migratory Ferruginous Hawk populations. However, unlike northern raptor populations, which may entirely desert a locality in low-prey years, breeding populations of each large raptor species were present even during unfavorable prey years in central Utah. In these instances, the response patterns of the nesting raptors are similar to the reproductive responses revealed by other studies of temperate raptor populations, with each raptor species increasing reproductive efforts in favorable prey years.

The response patterns of the central Utah breeding raptor populations may reflect the unique nature of the disturbed habitat. The dual environmental impact of overgrazing and predator control programs have produced a comparatively simplistic food web, characterized by the superabundance of a single prey species, the black-tailed jackrabbit, which exhibits strong fluctuations in density. This results in a local desert environment which in some respects resembles the northern tundra ecosystem, and which may in turn produce the raptor breeding responses discussed in this paper.

Summary

In the years 1966–1971 we studied the relationships between a collective breeding raptor population of Golden Eagles, Great Horned Owls, Ferruginous Hawks, and Red-tailed Hawks and its staple prey base, the black-tailed jackrabbit, in central Utah.

Densities of jackrabbits fluctuate widely in this area. Each raptor species responded functionally to these jackrabbit fluctuations, consuming proportionally greater amounts of this prey species in years of higher abundance. Each raptor species also responded numerically to jackrabbit fluctuations.

Two forms of numerical responses were observed: increased concentrations of raptors in favorable years, and increased reproductive efforts of breeding raptor populations, which also varied synchronously with jackrabbit abundance. Key factor analysis of raptor species densities suggest two major reproductive strategies, the tendency of pairs to breed in favorable years and refrain from breeding in low prey years, and a variation of clutch size, with maximum clutch size produced synchronously with jackrabbit density highs.

The relationship of the raptor species populations with their chief prey base is revealed by response patterns similar in respects to both North and temperate zone raptor populations, and may reflect the disturbed nature of the central Utah habitat.

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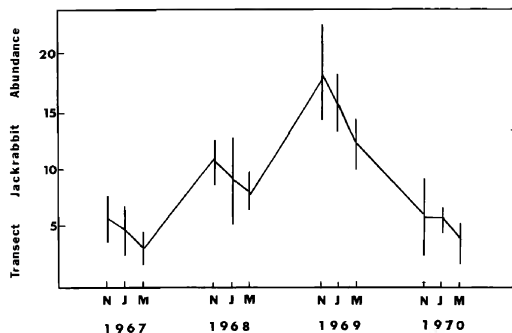


Figure 1. Transect counts of jackrabbit abundance on the central Utah study area, 1967-1970. Months presented for each year are November (N), January (J) and March (M). Vertical lines represent one standard deviation above and below average count.

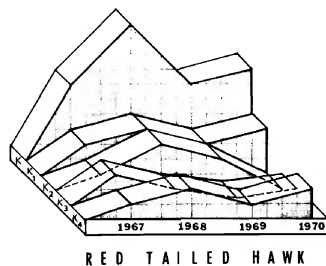
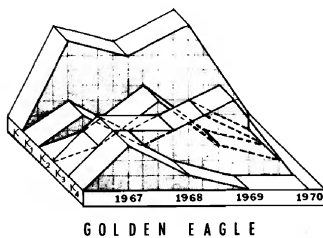
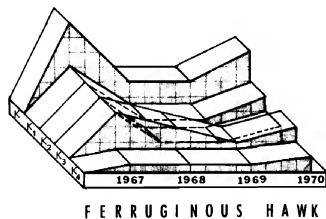
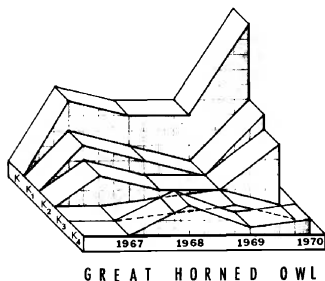


Figure 2. Graphs of key factor analysis for reproduction data of each large raptor species population on the intensive study area in central Utah, 1967-1970. Individual key factors as presented in text.